Thesis/
Reports
Farris,
C. A.

THE INFLUENCE OF SEED AVAILABILITY AND FIRE SEVERITY ON THE INITIAL POSTFIRE SEEDLING ESTABLISHMENT OF SUBALPINE CONIFERS IN CENTRAL IDAHO

Calvin A. Farris and Leon F. Neuenschwander
Department of Forest Resources, University of Idaho, Moscow, ID 83843

Susan L. Boudreau
Payette National Forest, McCall, ID 42393

ABSTRACT

Relatively little is known about the factors that determine the composition and density of postfire seedling establishment in subalpine forests following a fire. We studied the effects of fire severity and seed availability on the initial postfire seedling establishment of three subalpine conifers following the Corral-Blackwell Fire (1994) in central Idaho. Permanent plots were established in high severity burns (complete duff consumption), low severity burns (partial duff consumption), and unburned forests of composed of Engelmann spruce, subalpine fir, and lodgepole pine. Seedling establishment, first year survival, establishment efficiency, vegetation recovery, and seed fall were measured and compared between burn severities. Landscape level level seed availability was modeled using satellite imagery and GIS analysis. We found that fire severity had a significant influence on initial seedling establishment but that each species was affected differently. Two years after the fire lodgepole pine appeared to favor high severity burns, subalpine fir favored low severity burns, and Engelmann spruce showed no clear preference between high severity and low severity burns for the parameters investigated. Seed fall was strongly correlated with seedling establishment for all species in the burned plots except for subalpine fir in high severity burns. High temporal and spatial variation in fine scale and landscape level seed availability was observed in the study area and has important implications for long term recruitment. The complex interaction of burn severity and seed availability resulted in high variability in initial seedling establishment between and among species, and may have a long lasting influence on postfire community dynamics.

INTRODUCTION

Large fires are an infrequent but important stand initiating disturbance in Rocky Mountain subalpine forests (Turner and Romme 1994, Peet 1988). Postfire conifer establishment in these harsh environments can be highly variable across the landscape.

Prolific seedling establishment may occur immediately after a fire or it may occur sporadically over several decades (Jull 1992, Habeck and Mutch 1973, Stahelin 1942). Numerous biotic and abiotic factors have been documented to influence postfire recruitment in subalpine forests. These include micro site availability (Gracz 1989), competition (Agee and Smith 1984), seed availability (Huff and Agee 1991), fire behavior (Anderson and Romme 1991, Franklin and Laven 1991), topography (Romme and Knight 1981), pests and pathogens (Alexander 1984), climate (Agee and Smith 1984, Agee 1994, Little and Peterson 1992), and chance (Jull 1994). However, the relative importance of a particular factor can vary temporally and spatially, and those factors that are important during initial seedling establishment may differ from those that influence subsequent tree establishment (Little and Peterson 1992). This variability, in part, contributes to the complex vegetation mosaic typical of most subalpine landscapes.

The factors that control the density and composition of seedlings immediately after a fire and how they change over time are poorly understood. Most research on postfire succession has been conducted in older burns ($\geq$ 50 years) where observed recruitment patterns have been correlated with environmental variables or used to substitute space for time in a chronosequence (Rebertus et al. 1992). These approaches are useful for identifying regional and long-term controls over regeneration such as climate (Little et al. 1992) and for formulating generalizations about long-term successional dynamics (Rebertus et al. 1992, Aplet et al. 1988), but only inferences can be made about the initial postfire environment. Relatively little is known about initial postfire environments.

Two potentially important factors that vary over time are fire severity and seed availability. Fire severity is defined here as the downward penetration of heat into the

soil and is expressed indirectly by the amount of duff and litter consumed (Rowe 1983, Schimmel and Granstrom). Variation in fire severity creates diverse seedling substrates ranging from charred surface litter and duff to bare mineral soil. However, recolonizing vegetation, decomposition, and physical weathering alter the characteristics of the forest floor soon after a fire (White et al. 1996) so surface substrates that initially favor or inhibit seedling establishment may not persist. Seed availability is of obvious importance to postfire recruitment, but little is known about initial seed fall dynamics following large fires and how they influence recruitment. Spatial and temporal variation in postfire tree mortality following large fires (Galipeu 1997) may compound inherent variability in cone and seed production (Alexander 1984, Woodard et al. 1994) resulting in higher variability immediately after a fire. Such vagaries of seed availability across the landscape may be an important source of variation in postfire conifer recruitment.

In 1994 large wildfires burned several thousand hectares of subalpine forests in central Idaho. We initiated a long-term study to gather baseline data on initial seed fall and seedling establishment patterns and to monitor long-term successional pathways with respect to fire behavior. This paper reports the findings after two years. Our objectives were to 1) determine the role of fire severity on initial seedling establishment of subalpine conifers, 2) to determine the relationship between seed availability and seedling establishment in different burn severities, and 3) to model seed availability across the landscape.

METHODS

Study Area

The Corral-Blackwell Complex Fire was ignited by lighting on August 3, 1994 on

the Payette National Forest in central Idaho. It burned approximately 83,000 hectares before it was extinguished by precipitation on October 6, 1994. Elevations ranged from approximately 600 meters to 2,735 meters, but more than 85% of the burn occurred in subalpine forests above 1,800 meters. Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.) and lodgepole pine (*Pinus contorta* Doug. Ex Loud. Var *latifolia*) form extensive mixed subalpine forests between 1,850 m and 2,200 meters (Steele et al. 1981). Soils are generally moderate to well drained sandy loams of granitic origin Steele et al. 1981). A spruce beetle (*Dendroctonus rufipennis* Kirby) outbreak covered much of the study area prior to the fire (U.S. Forest Service 1995) resulting in variable mortality of large spruce (>40 cm) ranging from 30% to 100%.

Plot Selection

Sixteen permanent 30 x 30 meter plots were randomly established within the burn and georeferenced using a global positioning system (GPS). Four plots were established in high severity burns, four in low severity burns, and eight in unburned forests. High severity burns are areas where 100% of the litter, duff, and humus layer were consumed and low severity burns are areas where the surface litter was consumed but the duff and humus layer are left intact. All plots were established where crown fires consumed *all* overstory foliage. The overstory composition of each plot consisted exclusively of Engelmann spruce, subalpine fir, and lodgepole pine (minimum 30% basal area of each species). Similar aspects (250° to 290°), elevations (within 140 meters), and slopes (<30% on mid-slope positions) were chosen to control for topographic variability.

Field Procedures

Seed fall was sampled using 1 x 1 meter metal seed traps covered with a wire mesh screen. Eight to ten seed traps were randomly placed in each plot and seeds were collected and tallied by species throughout the Fall and in the Spring following snow melt (no tests were conducted to determine seed viability). All traps were in place by the end of September in 1994 (the year of the burn) and by September 1 in 1995. Seedling establishment was censussed in late October of 1995 and 1996 using a series of systematic belt transects so that the entire plot was surveyed. A first year seedling was considered established if it was alive at the end of October. The number of seedlings of each species and the age (first year or second year) were recorded within each transect. Grass and shrub cover was estimated in each plot in October of 1994, 1995, and 1996 using ocular estimates of the entire plot.

Data Analysis

Differences in seed fall and seedling establishment between burn severities was tested using a one way analysis of variance (ANOVA) and a Tukey Least Significantly Difference (LSD) multiple comparison (alpha = 0.05). The data did not meet the assumptions of normality so a square root transformation was performed on all count data. A Pearson Correlation test (Zar 1990) was used to determine if seed fall was correlated with first year seedling establishment. Correlation coefficients range from -1 to 1. A value of 1 indicates a strong positive correlation, a value of 0 indicates no correlation, and a value of -1 indicates a negative correlation between seed fall and seedling establishment. A Student's *t*-test was used to test whether the population parameter of coefficient values was significantly greater than zero.

First year seedling survival was calculated as the percentage of seedlings established in 1995 that were still alive at the end of the second growing season in 1996. Differences in survival between burn severities was tested with a one-way ANOVA. To attain a quantitative measure of relative germination efficiency, a seed to seedling ratio was calculated by dividing the number of seeds by the number of first year seedlings/m2. Lower ratios should indicate more favorable germination conditions than higher ratios. Shrub and grass cover in each plot was compared each year using the one way ANOVA and Tukey HSD test. Statistical analysis was performed using the SYSTAT statistical software package (release 6.1) for windows (Systat).

Landscape Seed Availability

Landscape seed availability was estimated by calculating the distance of lethally burned forests to the nearest potential live forest edge (seed wall) using ARC/INFO GRID. Postfire mortality patterns were classified at 30 meter resolution from Landsat Thematic Mapper satellite imagery using an unsupervised ISODATA classification procedure in ERDAS IMAGINE (Wirth et al. 1995). Four levels of fire intensity were delineated: 1) high intensity (complete crown consumption), 2) moderate intensity (complete mortality but canopy retains scorched foliage), 3) low intensity (little or no immediate foliage damage), and 4) unburned. Forests burned by high intensity and moderate intensity fires were classified as lethal. Unburned forests and forests burned by low intensity fire were assumed to be potential seed sources.

This assumption appeared valid one year after the fire but field observations during the second field season revealed very heavy mortality in low intensity burns. Subalpine fir and Engelmann spruce are highly susceptible to fires and even low intensity

burns are generally lethal (Crane and Fischer 1986). Delayed postfire mortality may continue for several years and can significantly alter initial landscape mosaics in subalpine forests (Ryan and Amman 1996). As a result, we also calculated the distance of lethally burned forests to the nearest seed source based on the assumption that at least half of the spruce and fir burned by low intensity fires would not survive. We used a prefire GIS coverage of vegetation to randomly classify fifty percent of spruce-fir forests burned by low intensity fires as lethal. The distance of lethal cells to the nearest live edge was recalculated and averaged over ten iterations to develop a final curve that accounts for postfire mortality.

RESULTS

Seed Fall

Seed fall varied considerably during the first two years after the fire (Table 1). Lodgepole pine accounted for the majority of seed fall in the burned plots both years, but differences between burned and unburned plots were not significant. Engelmann spruce and subalpine fir seed fall was significantly higher in the unburned plots than burned plots in 1995 but not in 1994. Few spruce and fir cones were observed in the study area in 1994 indicating that it was probably a poor seed year for both species. Spruce and fir seed production increased sharply in the unburned plots in 1995 but this did not correspond with an increase in the burned plots because the majority of mature spruce and fir in the burn died during the second summer. Despite high seed production by all species in 1995, seed fall was completely absent in three of the burned plots suggesting they may no longer be within the seed dispersal distance of living trees.

Seedling Establishment

Postfire seedling establishment was relatively low during the first two years but variability between plots was high (Table 2). After two years, lodgepole pine seedling densities in the burned plots ranged from 67 seedlings/hectares to 4,867 seedlings/hectare. Lodgepole pine seedling densities were highest in the high severity plots and lowest in the unburned plots (alpha = 0.05). Subalpine fir seedling densities ranged from 0 to 689 seedlings/hectare in the low severity plots, but no seedlings were found in the high severity plots. Differences between low severity and unburned plots were not significant. Engelmann spruce establishment did not differ significantly between the three burn substrates. Spruce seedling densities ranged from 0 to 1,822 seedlings/hectares in both the burned and unburned plots.

First Year Survival

Mean first year seedling survival was higher in the burned plots than the unburned plots for all three species (Figure 1). Lodgepole pine survival was highest in the high severity burns, but differences between low severity and unburned plots were not significant . Subalpine fir survival was significantly higher on low severity burns than unburned plots, but no seedlings were observed in the high severity plots in 1994 so we could not accurately compare survival among all three substrates. First year survival of Engelmann spruce was higher in the burned plots than the unburned plots but there was not a significant difference between high severity and low severity plots.

Seed Fall-Seedling Correlation

There was a strong positive correlation between seed fall and first year seedling

establishment in the burned plots during the first two years (Table 3). The only exception was subalpine fir in the high severity plots where seedling establishment was absent regardless of seed fall. Correlation coefficients (r) for all other species/severity combinations ranged from .84 to .98 ($p < 0.05$). In contrast, all three species showed no correlation between seed fall and seedling establishment in the unburned plots ($p > 0.05$). These results imply that seed availability is more closely associated with seedling establishment in burned areas than unburned areas.

Seed to Seedling Ratios

The lowest seed-seedling ratios for all species occurred in the burned plots suggesting that seedling establishment was more efficient in the burn (figure 2). These results are consistent with our findings of higher survival and higher seed toseedling correlations in burned plots. Seed to seedling ratios for lodgepole pine and Engelmann spruce were significantly lower in high severity plots than the low severity plots, but the lowest ratios for subalpine fir occurred in the low severity plots.

Postfire Grass and Shrub Cover

Differences in herbaceous and shrub cover between low severity and high severity burns were dramatic (Figure 3). Grasses and shrubs quickly resprouted following low severity burns, and increased from 0% to an average 12% just several weeks after the fire. Shrub and grass recovery was low in the high severity plots and first year cover remained near 0% in all plots. Average grass and shrub cover in low severity plots increased to 45% in 1995 and 65% in 1996, compared to just 7% and 19% on high severity plots. Bare mineral soil and ash covered the majority of high severity plots at the end of the

second year.

Landscape Seed Availability

The distance of lethally burned cells to the nearest live forest edge (potential seed source) ranged from 30 meters (adjacent) to 1,200 meters after the fire, with fewer than 5% of the cells at distances greater than 500 meters (Figure 4). Approximately 50% of the lethally burned forests were within 100 meters of a live edge and approximately 77% were within 200 meters. When delayed postfire mortality is accounted for these figures drop to 26% and 55% respectively, and the proportion of >500 meters of a live edge increases from 5% to 15%. These results indicate that landscape seed availability is influenced by both spatial and temporal heterogeneity of postfire mosaics.

DISCUSSION

Transient factors that influence postfire environments may have long lasting effects on long-term successional dynamics (McCune and Allen 1984). Our results indicate that seed availability and fire severity significantly influence initial seedling establishment and suggest that the specific characteristics of a fire rather than just the presence of fire are important in shaping postfire communities. This has important implications because the factors that control the occurrence and distribution of duff consumption and fire intensity (and thus seed availability) across the landscape during large wildfires are to a large degree stochastic. Large fire events that encompass a wide range of weather and topographic conditions can be expected to create more

heterogeneity across the landscape than smaller fires (Turner et al. 1993). Currently, the relative importance of initial seedling establishment patterns on the long-term structure and composition of postfire communities following large fires is poorly understood.

Postfire Seed Fall

The high correlation between seed fall and first year seedling establishment in burned plots suggest that initial postfire recruitment is largely a function of seed availability. In fact, for each species the plot with the seed input also had the highest seedling density . These results illustrate the limitations of examining seedling densities without knowledge of seed input. The absence of recruitment in many cases is likely due to a lack of propagules, whereas high seedling densities in an area may represent an abundant seed source rather than more favorable recruitment conditions. Species composition is also directly related to seed availability, which was evident by the fact that only four of the eight burned plots had seed from all three species during the first two years.

Just three years after the Corral-Blackwell Fire some distinct seed fall patterns have already emerged. Some burned areas lie beyond the seed dispersal distance of live trees and will not receive more seed for at least 15-40 years until existing seedlings (assuming they exist) mature to cone bearing age (Anderson and Romme 1991, Alexander 1984). Recruitment in these areas will be absent or poor regardless of other environmental conditions. In others areas, seed fall was virtually absent during the first year but increased significantly during the second year (especially spruce and fir),

indicating that the lack of first year seed was likely the result of a poor cone crop. First year spruce and fir seedling establishment in the burn might have been higher had the fire burned in 1995 during a bumper seed crop. The remaining areas received abundant seed fall both years and will likely exhibit continuous recruitment over time given a suitable substrates and climate.

The availability of seed in any area following a fire depends on a number of factors, including the spatial arrangement of lethal fires (Turner et al. 1994), the characteristics of the pre-fire vegetation (Alexander 1987), seed predation (Cameron and Jenkins 1988), and inherent variability in seed production of subalpine conifers (Alexander 1984). Although the importance of seed availability tree establishment is apparent, spatial and temporal variation in seed availability have rarely been considered explicitly in postfire successional models and these factors are often assumed to be constant. An important question to address is how long the correlation between seed fall and seedling establishment observed during the first two years of this study persist in different burn substrates?

Landscape Seed Availability

Models of conifer seed dispersal show that seed fall density drops sharply as a function of distance from seed source (Greene and Johnson1989) suggesting that tree recruitment patterns will also vary along a distance gradient from the nearest live edge. Large forest openings with diameters beyond the maximum seed dispersal distance may present barriers to postfire regeneration. Despite the extensive area burned by the Corral-

Blackwell Fire many unburned and low intensity patches were dispersed across the landscape. However, there were also a number of extensive crown fire patches (up to 2,000 ha) which were remarkably uniform in mortality.

The effective postfire seed dispersal distance (Alexander 1987) varies by species. McCaughey and Schmidt (1987) measured Engelmann spruce seed dispersal on ten sites in the Intermountain West (including study area) and found that while some seed dispersed as far as 200 m, 75% fell within 30 m and 95% fell within 120 m from the windward seed source. Similar patterns have been observed for subalpine fir in Colorado, which has slightly larger and heavier seed than spruce (Alexander 1987). Sufficient seed for adequate stocking of lodgepole pine usually does not occur beyond 67 m of a seed source (Alexander et al. 1983, Lotan and Critchfield 1990). A micrometerological model of conifer seed dispersal developed by Greene (1989) indicates that at 200 meter, a maximum of 1-4% of total seed fall in the forest can be expected. These figures imply that for subalpine forests in the study area, maximum seed fall will occur at distances <50 m from a live edge with progressively lower seed fall densities occurring from 50 m to 200 m. Openings with diameters >200 m are potential barriers to regeneration.

One year after the fire approximately 29% of the subalpine forests burned by lethal fires were within the maximum seed fall zone (<50 m of a live forested edge) and approximately 21% were beyond the maximum seed dispersal distance of 200 m (Figure 4). Approximately half of lethally burned forests were at intermediate distances (between 50 m and 200 m) where a sharp seed fall/seedling establishment gradient is expected.

Temporal changes in postfire mosaic caused by delayed mortality resulted in significant variation in seed availability (dashed line, Figure 4). In our simulation, the proportion of lethally burned area <50 m of a live edge decreased from 29% after the fire to as low as 15% after mortality, and the area greater than the maximum seed dispersal distance increased from 23% to as high as 46% in one scenario. Of course, mortality in spruce-fir stands burned by low intensity will not always be 100%, but field observations two years after the burn indicate that a significant decrease in basal area is likely. Since basal areas is positively correlated to both seed production (Stromberg and Patten 1993) and seed dispersal (McCaughey and Schmidt 1987, Alexander 1984) of spruce and fir, decreases in seed availability in those areas is likely.

Galipeau et al. (1997) examined recruitment patterns in a sixty-eight year boreal forest burn and found that the density and basal area of white spruce (*Picea glauca* (Moench)Voss) and balsam fir (*Abies balsamea* (L.) Mill.), two non-serotinous conifers, was highest in areas ≤60 meters of an unburned zone and decreased significantly as the distance to the nearest unburned zone increased. We hypothesize that similar variation in recruitment patterns will occur along distance gradients represented in Figure 4. Although only 21% of lethally burned area was greater than 200 m from a live edge after the fire, this represents an area of approximately 9,000 hectares. Individual trees or small groups of trees at scales finer than the resolution of the satellite imagery will invariably be scattered throughout the burn providing an important source of propagules in most areas and first year seed from serotinous cones (assuming they are present) may also contribute. However, recruitment in such cases differs compared to areas near continuous

seed walls (Agee and Smith 1984), tending to occur as "advancing waves" in which small groups or individuals establish at relatively short distances from parent trees (Huff and Agee 1991, Galipeau et al. 1997). Such spatial and temporal variability in seed availability across the landscape is an important consequence of large fire events.

Fire Severity

Given a suitable seed source, fire severity appears to have an important species specific influence on initial seedling establishment patterns. Fire severity affected seedling density by influencing key variables important to recruitment such as survival, establishment efficiency, vigor, and postfire competition. At the end of the second year lodgepole pine appeared to favor high severity burns, subalpine fir appeared to favor low severity burns, and Engelmann spruce did not show a clear preference between high and low severity burns. The effect of fire severity on seedling establishment seems to be the result of a better germination substrate and early establishment environment. Whether these differences are the result of different chemical and physical characteristics between the different substrates (e.g. charred duff versus ash or bare mineral soil) or indirect factors such as plant competition and herbivory could not be determined, but it is likely a combination of both (Gracz 1989).

The degree to which fire severity produces observable differences in seedling density and composition may vary over time however. For example, lodgepole pine establishment may not initially differ between burn substrates but higher mortality in low severity plots will eventually result in differences between high and low severity burns.

Another example is that although low severity plots required nearly three times as many lodgepole pine seeds to produce a first year seedling than high severity plots, seedling densities may not differ if seed fall is greater on low severity plots.

Competition with grasses and shrubs has also been shown to inhibit conifer recruitment following fire (Agee 1984). Differences in grass and shrub cover was one of the most visible differences between low and high severity plots two year after the burn. The differences in recovery of herbaceous and shrub vegetation between low severity plots during the second postfire year appeared to directly influence the establishment patterns and vigor of conifers. Qualitative observations of seedling height and vigor suggest that seedlings in opening were taller and fuller compared to seedling beneath shrub or grass canopies. We are currently studying seedling height and widths in different levels of fire severity and herbaceous cover..

At least initially, high severity burns appeared to be unfavorable for subalpine fir seedling establishment. This is consistent with the findings of Alexander (1987) who concluded that subalpine fir regeneration was more favorable on mineral soils at lower elevations but that duff at higher elevations provided insulation. It has also been hypothesized that subalpine fir requires safe micro sites such as down logs and shrubs to moderate extremes in temperature and moisture (Little and Peterson 1992, Veblen (1986). These conditions appear to exist much earlier in low severity burns than high severity burns. Numerous logs (in various stages of decay and/or char) and shrubs were present on low severity sites immediately after the fire but were virtually nonexistent on high severity sites. Continued monitoring will be necessary to determine how long subalpine

fir is absent on high severity burns where a seed source is present.

The potential importance of fire severity to postfire conifer recruitment has important implications because it is rarely addressed in postfire successional models. Fire intensity has most commonly been used to describe fire effects on potential vegetation development because of its visible effects on stand structure and landscape patterns, and the fact that it can be easily delineated for many years after the fire. In contrast, it is difficult or impossible to accurately reconstruct duff consumption patterns in old burns because of weathering and vegetation development. Our field observations indicated that there was a weak correlation between fire intensity and fire severity, especially in large crown fire patches. It is conceivable that differences in fire severity can result in variable recruitment even where fire intensity is uniform (e.g. low severity burns observed within a homogenous crown fire patch). Different combinations of fire intensity and fire severity observed throughout the Corral-Blackwell Fire should be monitored over time.

SUMMARY AND CONCLUSIONS

The Corral-Blackwell Fire is an example of a single, infrequent disturbance event that will shape the landscape mosaic for hundreds of years. Spatial variation in fire behavior characteristics will likely be an important source of postfire recruitment variability. We have shown that fire severity and seed availability (at the stand and landscape level) influence initial postfire seedling establishment patterns in the mixed subalpine forests of central Idaho. These factors interact, making simple comparisons of

seedling densities between burn substrates difficult to interpret. In some areas, continuous recruitment will continue for many years and initial seedling establishment patterns observed in this study may ultimately be masked by future regeneration events (either continuous or pulses). In other areas however (e.g. HS 4), initial recruitment patterns may remain evident for a long time (probably until the next stand replacing disturbance) due to a lack of propagules or suitable seedling substrates. It is likely that many observed differences in stand structure and composition in older forests are the result of initial recruitment patterns which have persisted. Long term monitoring at the landscape level will be necessary to ultimately determine the influence of early recruitment patterns on long-term succession. Such knowledge will be valuable for refining our understanding of long-term successional dynamics and for assessing postfire management strategies.

Acknowledgments: This research was supported in part by funds provided by the Intermountain Research Station, Forest Service, U.S. Department of Agriculture and McIntire-Stennis, College of Forest, Wildlife, and Range Sciences, University of Idaho.

able 1. Estimated seed fall (seeds/ha) of lodgpole pine, Engelmann spruce, and ubalpine fir during the first two years following the Corral-Blackwell Fire.

		seeds/hectare					
burn		*Lodgepole Pine*		*Engelmann Spruce*		*Subalpine Fir*	
severity	*plot no.*	*1994-95*	*1995-96*	*1994-95*	*1995-96*	*1994-95*	*1995-96*
unburned	*ub1*	285,000	85,000	40,000	902,500	95,000	830,000
	ub2	100,000	155,000	120,500	1,462,500	35,000	402,000
	ub3	85,000	120,000	5,000	237,500	70,000	242,500
	ub4	222,500	97,500	22,500	232,500	10,000	345,000
low	*ls1*	170,000	20,000	30,000	97,500	17,500	35,000
	ls2	195,000	65,000	87,500	0	77,500	0
	ls3	520,000	5,000	0	0	12,500	0
	ls4	102,500	25,000	7,500	90,000	5,000	77,500
high	*hs1*	205,000	20,000	25,000	37,500	50,000	85,000
	hs2	322,500	87,500	20,000	47,500	35,000	120,000
	hs3	12,500	0	0	0	12,500	0
	hs4	---	2,500	---	0	---	0

Table 2. First and second year seedling densities (seedlings/ha) in unburned, low severity, and high severity burn plots in the Corral-Blackwell Fire. Seedling establishment was inventoried by censusing each 30 x 30 m plot with a series of systematic transects in October and November of each year.

		seedlings / hectare								
burn		*Lodgepole Pine*			*Engelmann Spruce*			*Subalpine Fir*		
severity	*plot no*	*1995**	*1996**	***TOTAL*****	*1995**	*1996**	***OTAL*****	*1995**	*1996**	***OTAL*****
nburned	*ub1*	0	89	89	44	267	267	67	156	156
	ub2	89	0	22	0	0	0	67	489	511
	ub3	111	133	133	733	1,200	1,400	467	800	978
	ub4	156	0	44	67	333	356	0	311	333
	ub5	356	67	67	22	400	400	0	311	311
	ub6	89	0	0	0	22	22	0	44	44
	ub7	67	22	22	0	156	156	89	67	67
	ub8	0	---	---	0	---	---	22	---	---
low	*ls1*	1,356	89	289	267	667	756	311	689	822
	ls2	1,978	311	533	778	0	311	667	44	356
	ls3	3,978	67	933	0	0	0	89	89	111
	ls4	689	44	133	44	267	267	44	311	244
high	*hs1*	2,400	222	2,156	244	267	378	0	0	**0**
	hs2	4,867	1,089	4,667	1,822	644	1,444	0	0	**0**
	hs3	222	22	200	0	0	0	0	0	**0**
	hs4	2,022	0	1,933	0	0	0	0	0	**0**

* first year seedling establishment only

** the total number of live seedlings (both first and second year) present at the end of the second post-fire year (1996)

Table 3. Pearson correlation coefficients showing the relationship between seed fall and seedling establishment during the first years after the fire. Coefficient values range from -1 to 1. A value of 0 indicates no association seed fall and seedling establishment, a value of 1 indicates a positive association, and a value of -1 indicates a negative association.

	Seed-Seedling Correlation Coefficient (*r*)					
	1994-95			1995-96		
	Unburned	Low Severity	High Severity	Unburned	Low Severity	High Severity
lodgepole pine	-0.298	0.984*	0.988*	0.391	0.91**	0.96*
Englemann Spruce	0.221	0.964*	0.972	0.21	0.974*	0.921**
Subalpine Fir	0.315	0.918**	0.192 †	0.493	0.843	0

* $p < 0.05$

** $p < 0.10$

† only one seedlings

Figure 1. Average first year seedling survival of lodgepole pine, Engelmann spruce, and subalpine fir in unburned, low severity, and high severity burns. Survival was calculated as the percentage of first year seedlings in 1995 (Oct.) that were still alive in 1996 (Nov.). Percentages below are the overall average (and standard error) of individual plot means.

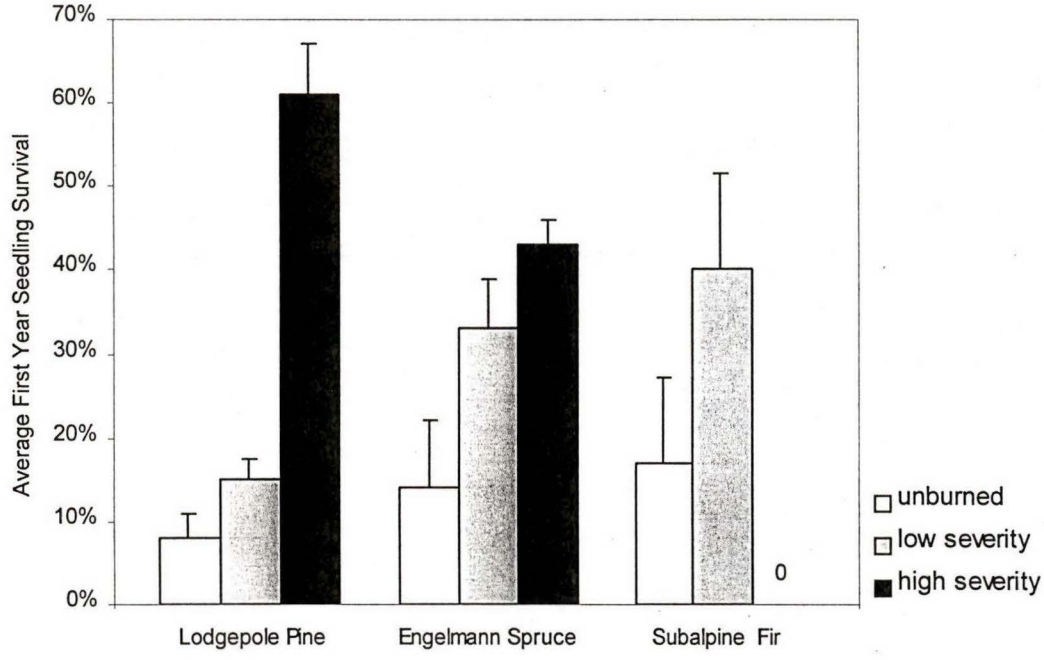
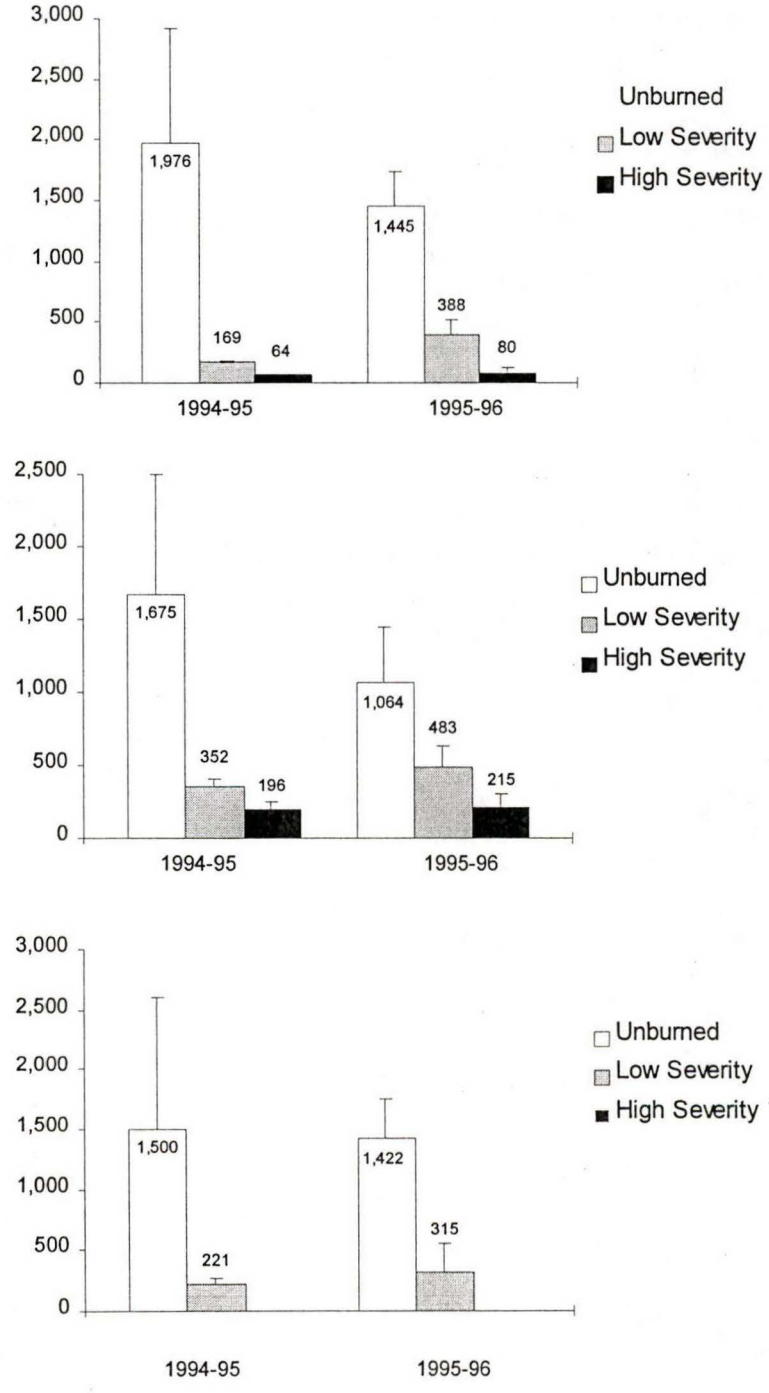


Figure 2. Average seed to seedling ratio (and standard errors) for first and second year lodgepole pine, Engelmann spruce, and subalpine fir seedlings in different burn severities. Ratios were derived for each plot by dividing the number of seeds/ha by the number of first seedlings/ha each year. Lower ratios indicate for favoreable germination conditions.



* Ratios were not calculated because only one seedling was observed during the two year period

Figure 3. Percent cover (mean and standard error) of shrubs and grasses in high severity, low severity, and unburned plots following the Corral-Blackwell Fire. All plots burned before September 6, 1994 and had 0% cover after burning. Estimates were taken on October 31 of each year.

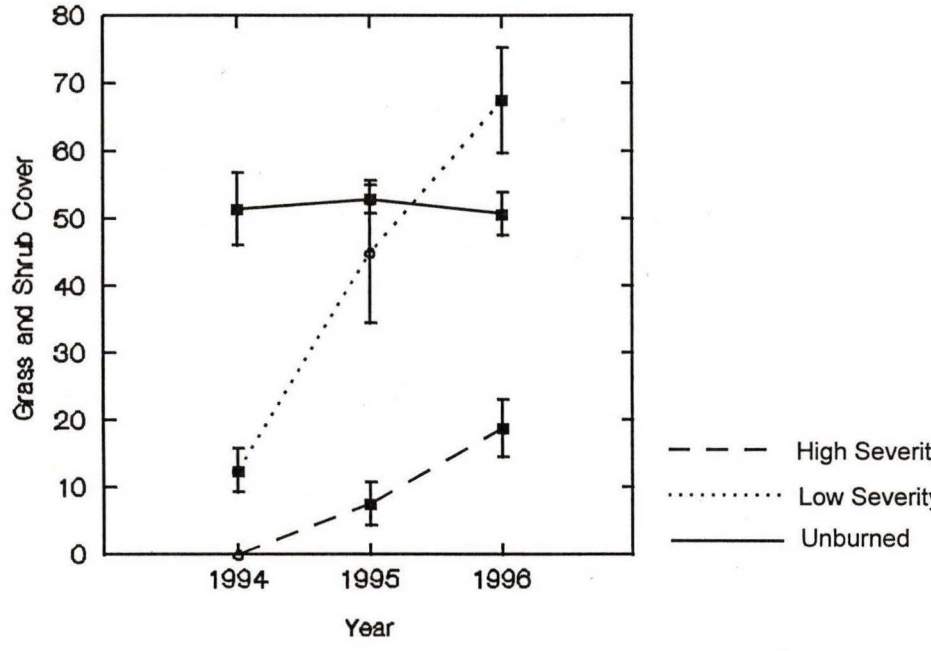
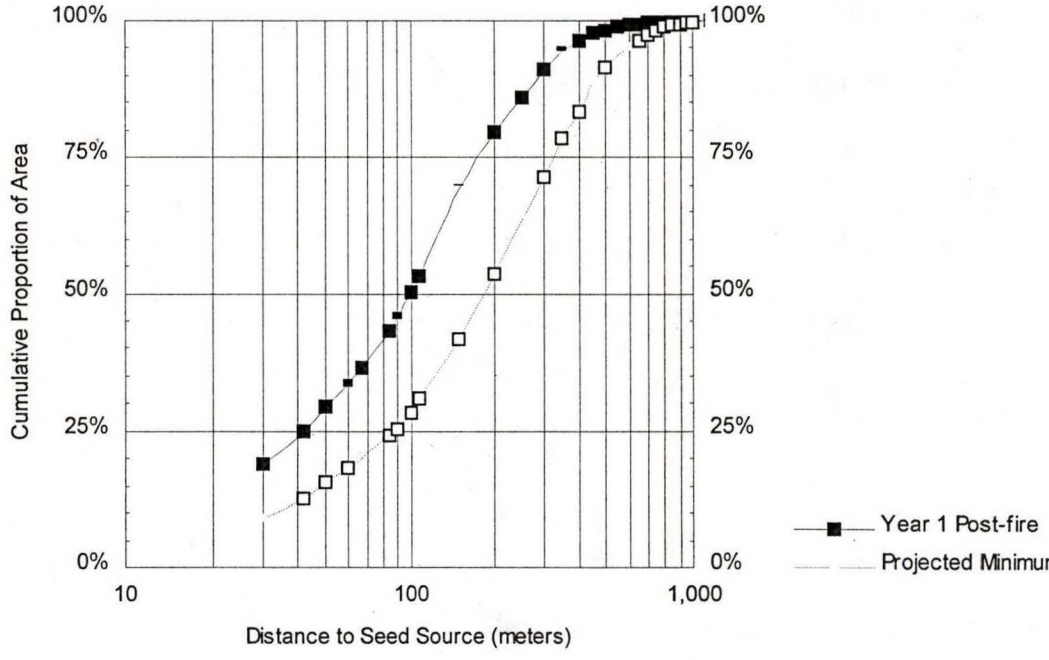


Figure 4. Model of the distance of subalpine forests burned by lethal fires to the nearest seed source (live forested edge), represented as a cumulative proportion of area burned. The Year 1 Post-fire estimate is the distance of moderate and high intensity fires from the nearest unburned or low intensity patch after the fire. The projected minimum estimate assumes the spruce-fir forests that burned with low intensity fire suffers mortality is no longer a suitable seed source in the future.



LITERATURE CITED

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Covelo, CA. 493 pp.

Agee, J.K. and L. Smith. 1984. Subalpine tree reestablishment after fire in the Olympic Mountains, Washington. Ecology 65(3):810-819.

Alexander, R. R. 1987. Ecology, silviculture, and management of the Engelmann spruce-subalpine fir type in the central and southern Rocky Mountains. United States Forests Service, Agricultural Handbook 659. Washington D.C.

Alexander, R.R., J.E. Lotn, M.J. Larson, and L.A. Volland. 1983. Lodgepole Pine. *In* R.M. Burns (tech. compiler). Silvicultural systems for the major forest types of the United States. USDA Forest Service, Agriculture Handbook No. 445. Pp. 59-63.

Anderson, J.E. and W.H. Romme. 1991. Initial floristics in lodgepole pine (*Pinus contorta*) forests following the 1988 Yellowstone fires. Int. J. Wildland Fire 1(2):119-124.

Cameron, D.E. and J.J. Jenkins 1988. Engelmann spruce cone losses caused by insects in northern Utah in a year of low cone production. Great Basin Naturalist 48(4):508-511.

Crane, M.F. and Fischer, W.C. 1986. Fire ecology of the forest habitat types of central Idaho. USDA For. Ser. GTR-INT-218. 86 pp.

Franklin, T.L. and R.D. Laven. 1991. Fire influences on central Rocky Mountain lodgepole pine stand structure and composition. In Proceedings: 17th Tall Timbers Fire Ecology Conference. Tall Timbers, Tallahassee, Fla. 183-196.

Fryer, G.I. and E.A. Johnson. 1988. Reconstructing fire behavior and effects in a subalpine forest. J. Of App. Ecology 25:1063-1072.

Galipeau, C. D. Kneeshaw, and Y. Bergeron. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. 27:139-147.

Greene, D.F. 1989. The aerodynamics and dispersal of plumed and winged seeds. PhD dissertation, University of Calgary, Canada.

Greene, D.F. and E.A. Johnson 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70:339-347.

Habeck, J.R. and R.W. Mutch. 1973. Fire-dependent forests in the northern Rocky Mountains. Wuat. Res. 3:408-24

Huff, M.H. and J.K. Agee. 1991. Subalpine forest dynamics after fire in the Pacific northwest national parks. Nat. Park. Ser., Coop. Park Studies Unit. Univ. Of Wash, Seattle. 62 pp

Gracz, M.B. 1989. Reestablishment of *Abies lasiocarpa* after fire in the Pacific Northwest. M.S. thesis, University of Washington, Seattle.

Johnson, E.A. and G.I. Fryer. 1986. Historical vegetation change in the Kananaskis Valley, Canadian Rockies. *Canadian Journal of Botany* 65:853-858.

Jull, Michael James. 1992. Long-term stand dynamics in high-elevation Engelmann spruce-subalpine fir forests. MSC thesis, University of British Columbia, Vancouver, B.C. 163 pp.

Little, R.L., D.L. Peterson, and L.L. Conquest. 1994. Regeneration of subalpine fir (*Abies lasipcarpa*) following fire: effects of climate and other factors. Can. J. For. Res. 24:934-944.

Lotan, J.E. and W.B. Critchfield. 1990. Lodgepole Pine. *In* R.M. Burns and B.H. Honkala. Silvics of North America: Volume 1, Conifers. USDA Forest Service, Agriculture Handbook No. 654. Pp.302-315.

Lotan, J.E. 1975. The role of cone serotiny in lodgepole pine forests. *In* Baumgartner, D.M., ed. Management of lodgepole pine ecosystems: proceedings of the symposium, October 9-11, 1973. Pullman, WA. Washington State University, Cooperative Extension Service, Pullman, WA. Pgs 471-496.

McCaughey, W.W., and W. Schmidt. 1987. Seed dispersal of Engelmann spruce in the Intermountain West. Northwest Science 61(1):1-6.

McCune, B. And T.F.H. Allen. 1984. Will similar forests develop on similar sites? Can. J. Bot. 63:367-376.

Payette National Forest, McCall Ranger District. 1991. Final environmental impact statement for the accelerated Engelmann spruce harvest for Brush Creek, Hendricks Creek, and Copet Creek salvage timber sales, Valley and Idaho Counties, Idaho. Responsive agency: USDA Forest Service, McCall, ID. Payette National Forest, McCall Ranger District.

Rebertus, A.J., T.T. Veblen, L.M. Rovvers, and J.N. Mast. 1992. Structure and dynamics of old-growth Engelmann spruce-subalpine fir in Colorado. *In* Old-Growth Forests in the Southwest and rocky Mountain Regions: Proceedings of a Workshop. USDA For. Ser. GTR-RM-213. Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO. 139-151.

Romme, W.H. and D.H. Knight. 1981. Fire frequency and subalpine forest succession along a topographic gradient in Wyoming. Ecology 62(2): 319-326.

Rowe, J.S. 1983. Concepts of fire effects on plant individuals and species. *In* R.W. Wein and D.A. MacLean, eds. The role of fire in northern circumpolar ecosystems. John Wiley, New Yourk, N.Y., USA. Pp 135-154.

Ryan, K.C., and G.D. Amman. 1996. Bark beetle activity and delayed tree mortality in the Greater Yellowstone Area following the 1988 fires. *In* The ecological implications of fire in Greater Yellowstone. Greenlee, J.M. (ed.). International Association of Wildlife Fire, Farifiel, WA.

Stahelin, R. 1943. Factors influencing the natural restocking of high altitude burns by coniferous trees in the central Rocky Mountains. Ecology 24(1):19-30.

Steele, R., R.D. Pfister, R.A. Ryker, and J.A. Kittams. 1981. Forest habitat types of central Idaho. USDA For. Ser. Gen. Tech. Rep. INT-114. Intermountain Research Station, Ogden, UT. 138 pp.

Stromberg, J.C. and D.T. Patten. 1993. Seed and cone production by Engelmann spruce in the Pinaleno Mountains, Arizona. J. Of the Arizona-Nevada Academy of Science. 27:79-88.

Turner, M.G. and W.H. Romme. 1995. Landscape dynamics in crown fire ecosystems. Landscape Ecology 9(1):59-77.

Turner, M.G., W.H. Romme, R.H. Gardner, R.V. O'Neill, and T.K. Kratz. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes.

Turner, M.G., W.W. Hargrove, R.H. Gardner, and W.H. Romme. 1994. Effects of fire on landscape heterogeneity in Yellowstone national Park, Wyoming. Journal of Vegetation Science 5:731-742.

White, J.D., K.C. Ryan, C.C. Key, and S.W. Running. 1996. Remote sensing of forest fire severity and vegetation recovery. Int. J. Wildland Fire 6(3):125-136.

Wirth, T. J. Powell, P. Maus, H. Lachowski, R. Morrow, and B. Sanders. 1995. A comparison of landsat thematic mapper and high altitude color infrared aerial photography to map burn intensity on the Payette National Forest. Report to the remote sensing steering committee. USDA Forest Service, Payette National Forest. McCall, ID.

Woodard, A.H., D.G. Silsbee, and J.E. Means. 1994. Influence of climate on radial growth and cone production in subalpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Can. J. For. Res. 24(6):1133.

Zar, J.H. 1984. Biostatistical Analysis (2nd edition). Prentice-Hall, Inc. Englewood Cliffs, N.J. 718 pp.